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Floral development and floral phyllotaxis in *Anaxagorea* (Annonaceae)

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• *Background and Aims Anaxagorea* is the phylogenetically basalmost genus in the large tropical Annonaceae (custard apple family) of Magnoliales, but its floral structure is unknown in many respects. The aim of this study is to analyse evolutionarily interesting floral features in comparison with other genera of the Annonaceae and the sister family Eupomatiaceae.
• *Methods* Live flowers of *Anaxagorea crassipetala* were examined in the field with vital staining, liquid-fixed material was studied with scanning electron microscopy, and microtome section series were studied with light microscopy. In addition, herbarium material of two other *Anaxagorea* species was cursorily studied with the dissecting microscope.
• *Key Results* Floral phyllotaxis in *Anaxagorea* is regularly whorled (with complex whorls) as in all other Annonaceae with a low or medium number of floral organs studied so far (in those with numerous stamens and carpels, phyllotaxis becoming irregular in the androecium and gynoecium). The carpels are completely plicate as in almost all other Annonaceae. In these features *Anaxagorea* differs sharply from the sister family Eupomatiaceae, which has spiral floral phyllotaxis and ascidiate carpels. Flat stamens and the presence of inner staminodes differ from most other Annonaceae and may be plesiomorphic in *Anaxagorea*. However, the inner staminodes appear to be non-secretory in most *Anaxagorea* species, which differs from inner staminodes in other families of Magnoliales (Eupomatiaceae, Degeneriacae, Himantandraceae), which are secretory.
• *Conclusions* Floral phyllotaxis in *Anaxagorea* shows that there is no signature of a basal spiral pattern in Annonaceae and that complex whorls are an apomorphy not just for a part of the family but for the family in its entirety, and irregular phyllotaxis is derived. This and the presence of completely plicate carpels in *Anaxagorea* makes the family homogeneous and distinguishes it from the closest relatives in Magnoliales.

Key words: *Anaxagorea*, Annonaceae, Magnoliales, Magnoliidae, basal angiosperms, carpels, complex whorls, floral phyllotaxis, inner staminodes, stamens, tepals.

INTRODUCTION

Anaxagorea is a genus of special phylogenetic interest in the large (112 genera, 2440 species; Couvreur *et al.*, 2011) tropical Annonaceae (custard apple family; Magnoliales) because it is sister to the remainder of the family, a position first found in structural cladistic analyses (Doyle and Le Thomas, 1994, 1996) and later supported by molecular analyses (van Zuilen, 1996; Doyle *et al.*, 2000, 2004; Sauquet *et al.*, 2003; Richardson *et al.*, 2004; Surveswaran *et al.*, 2010; Couvreur *et al.*, 2011). A detailed discussion of morphological features and their evolution within the genus, also including some floral characters, was provided by Scharaschkin and Doyle (2005, 2006). The beetle pollination, florivory and heterodichogamy in the genus have been the subject of study (Maas-van de Kamer, 1993; Armstrong and Marsh, 1997; Jürgens *et al.*, 2000; Silberbauer-Gottsberger *et al.*, 2003; Collier and Armstrong, 2009; Teichert *et al.*, 2011). However, early floral development and floral phyllotaxis of *Anaxagorea* have not been studied, and many other aspects of floral structure remain poorly known. This is particularly critical in light of the survey of floral development among 12 genera of Annonaceae not including *Anaxagorea* (Xu and Ronse De Craene, 2010).

Floral phyllotaxis in those Annonaceae so far studied is whorled, with simple or complex whorls, or irregular (Leins and Erbar, 1980, 1996; Endress, 1986, 1987; Ronse De Craene and Smets, 1990; Endress and Doyle, 2007; Saunders, 2010; Xu and Ronse De Craene, 2010). Despite indications of spiral floral phyllotaxis in the general literature (e.g. Cronquist, 1981; van Heusden, 1992; Kessler, 1993; Takhtajan, 1997), no single documented case of regular spiral floral phyllotaxis is known in the family. Eupomatiaceae, which are sister to Annonaceae, have spiral floral phyllotaxis (Endress, 2003), so knowing the phyllotaxis pattern in *Anaxagorea*, sister to the rest of the Annonaceae, is of special interest for evolutionary interpretation of this character.

Another feature of interest is the presence of inner staminodes in *Anaxagorea* (Baillon, 1868*b*; Fries, 1940), which are absent in most other Annonaceae, except for some *Xylopia* species (Fries, 1940; van Heusden, 1992). Inner staminodes also occur in Eupomatiaceae where they play an important biological role with their movements and secretions (Endress, 1984*a*, *b*; Armstrong and Irvine, 1990). In *Anaxagorea* these staminodes are less conspicuous and, although they appear to be secretory in certain species (Scharaschkin and Doyle, 2006), their structure has not been studied in detail.

Lastly the gynoecium is of interest in *Anaxagorea* because it is one of the few genera in Annonaceae in which the carpels have been reported to have an ascidiate base (*A. luzonensis*; Deroin, 1988), resembling Eupomatiaceae in this feature (Endress, 1977; Igersheim and Endress, 1997). In addition, *Anaxagorea* is the only genus in Annonaceae (and Magnoliales) with ballistic seed dispersal (van Setten and Koek-Noorman, 1992). However, developmental studies of the gynoecium are lacking. The availability of specimens makes it possible to resolve some of these morphological questions for *Anaxagorea*, which is the aim of this study.

MATERIALS AND METHODS

Anaxagorea crassipetala Hemsl. is a small understorey tree of the primary wet forest in Costa Rica. The peak flowering season for this species is October and November. Floral specimens of diverse developmental stages were field collected in October 2007 at the La Selva Biological Station by J.E.A. (voucher: ISU), fixed in FAA (formalin/acetic acid/alcohol), and 2 weeks later transferred to 70 % ethanol for storage. Fresh anthetic flowers were partially dissected and treated with a 1 % neutral red solution to help identify any active secretory structures.

For scanning electron microscopic observation the specimens were variously dissected, critical point dried, sputter-coated with gold and examined with a Hitachi S-4000. Material for sectioning was infiltrated and embedded in Histomount, sectioned at 7 μm with a Microm HM 355 rotary microtome, and stained with Ruthenium red and toluidine blue, applying the technique described by Igersheim and Cichocki (1996).

Herbarium material of two additional species, *Anaxagorea acuminata* (Dunal) A. DC. (J.C. Lindeman 6868) and *A. luzonensis* A.Gray (A.D.E. Elmer 17739), both located at Z, was cursorily studied for floral phyllotaxis.

RESULTS

Inflorescences and flowers

Anaxagorea crassipetala bears inflorescences in the axils of new leaves. The inflorescences have a terminal flower and one (or more) lateral cyme, and are thus thyrsoid (for this term, see Müller-Doblies and Müller-Doblies, 1987; Endress, 2010). Their persistence for many seasons after leaf senescence results in ramiflory or cauliflory. At anthesis the flowers are some 25–28 mm long and pendent (Fig. 1A). Three alternating perianth whorls are evident; the outermost is sepaloid and persistent, the inner two are petaloid, creamy-white, and abscise along with the androecium at the end of the 24 h anthesis. In particular, the tepals of the second perianth whorl are extremely fleshy, constituting nearly two-thirds of the floral biomass (Armstrong and Marsh, 1997).

Floral phyllotaxis, organ number and merism

Regularly developed flowers have nine tepals, 42 stamens (the innermost 6–12 of them sterile: inner staminodes) and 19 carpels (Figs 2F and 3A, B). The three tepal whorls are trimerous. The first androecial whorl consists of six stamens in double positions, these double positions alternating with the three inner tepals (for terminology of double positions, see Staedler and Endress, 2009). The second whorl has six stamens alternating with those of the first whorl. In total there are seven whorls of six stamens (including the staminodes). This pattern continues in the gynoecium containing three whorls of six carpels. The organs of the androecium and gynoecium form 12 regular orthostichies (Fig. 3A). The centre of the gynoecium is somewhat variable, depending on the space left at the remaining floral apex. Commonly an additional carpel forms in the centre of the innermost carpel whorl (Figs 2F and 4A). In other flowers, the innermost gynoecial whorl has <6 carpels and there is no organ in the centre.

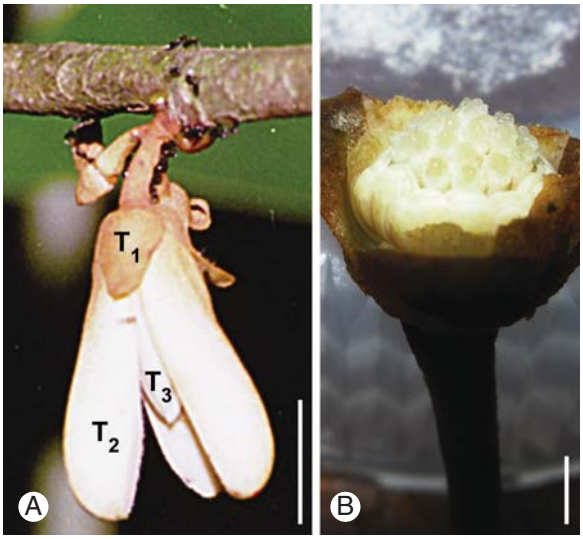

FIG. 1. *Anaxagorea crassipetala*. (A) Flower at anthesis. T_1, tepal of first whorl; T_2, tepal of second whorl; T_3, tepal of third whorl. (B) Androecium and gynoecium at early anthesis, with glistening gelatinous stigmas. Scale bars: (A) = 1 cm; (B) = 1 mm.

Perianth

A flower is preceded by a sheathing bract (Fig. 2A, B). The first tepal alternates with this bract (Fig. 2B). The first three tepals originate with very short plastochrons (Fig. 2B); the plastochrons are so short that the organ sequence may even be difficult to establish. This is also true for the organs within the subsequent two perianth whorls (Fig. 2C, D). However, the plastochron between whorls is conspicuous. At the time the outer stamens are initiated the inner three tepals are still much smaller than the outer six tepals; they are almost horizontally directed and are closely appressed to the floral apex (Fig. 2E). At anthesis, tepal aestivation is approximately valvate in the first whorl (Fig. 2C). The upper part of the tepals in the second and third whorl is also valvate (Fig. 1A); however, the tepals are open at their base but, when the tepals of the second and third whorl are viewed together, they collectively also form a valvate pattern (Figs 2E and 3B).

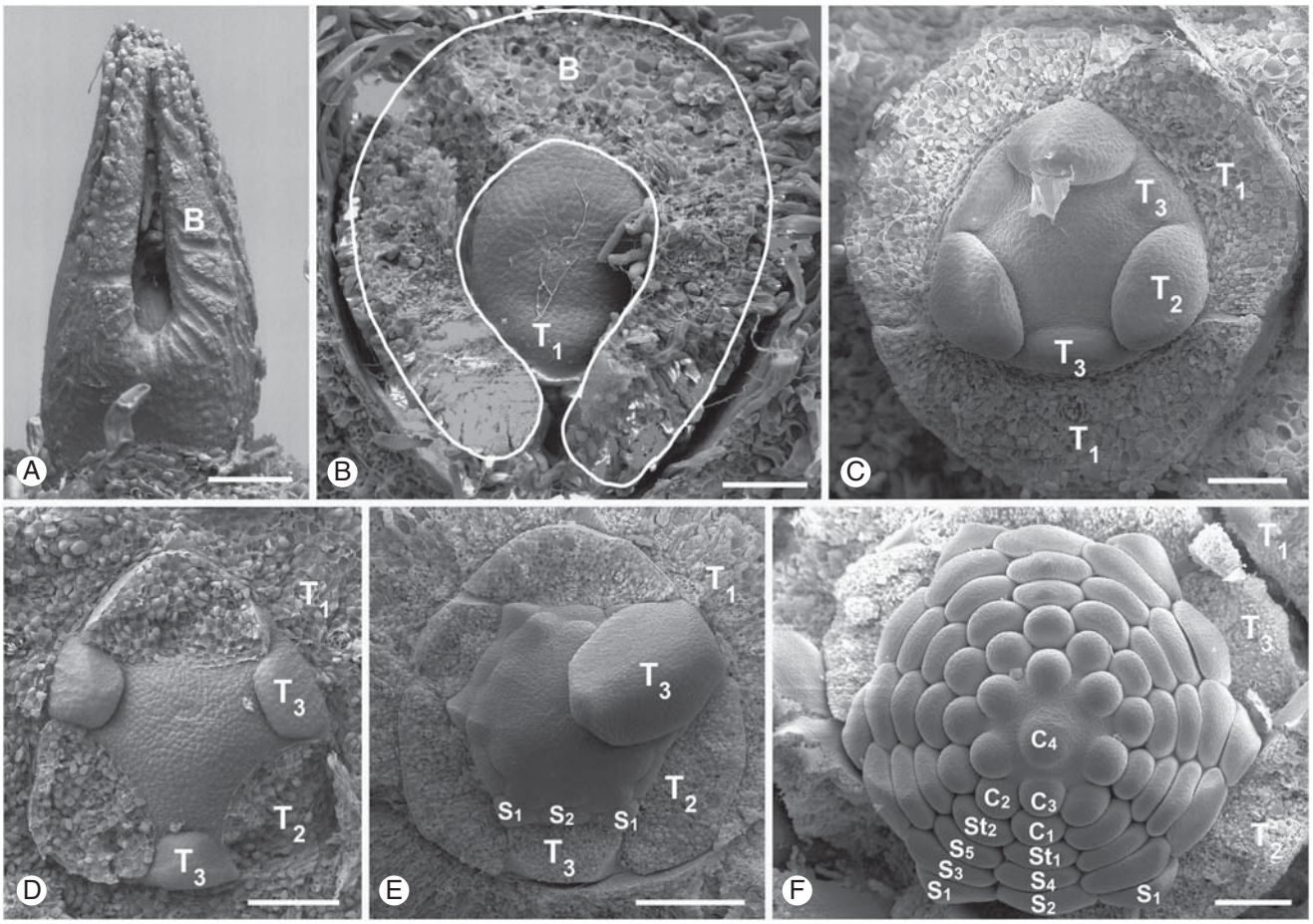

FIG. 2. *Anaxagorea crassipetala*. Scanning electron microscopy micrographs. (A) Sheathing bract surrounding a young flower (flower hidden), from the ventral side (the bract has imprints of hairs from an outer, removed bract). (B) Young flower with the first tepal whorl being initiated; first tepal primordium (marked) positioned opposite the sheathing bract (sheathing bract removed, outlined with a white line). (C) Young flower with all three tepal whorls present, tepals of third whorl just initiated (tepals of first whorl removed). (D) Young flower with all three tepal whorls present, tepals of third whorl somewhat older (tepals of first and second whorl removed). (E) Young flowers with stamens being initiated, stamens of outer stamen whorl with double positions (all tepals except one of the third whorl removed). (F) Young flower after initiation of all organs (all tepals removed). Abbreviations: B, bract; C_1, carpel of first whorl; C_2, carpel of second whorl; C_3, carpel of third whorl; C_4, central carpel; S_1, stamen of first whorl; S_2, stamen of second whorl; S_3, stamen of third whorl; S_4, stamen of fourth whorl; S_5, stamen of fifth whorl; St_1, staminode of first whorl; St_2, staminode of second whorl; T_1, tepal of first whorl; T_2, tepal of second whorl; T_3, tepal of third whorl. Scale bars: (A–D) = 50 μm; (E, F) = 100 μm.

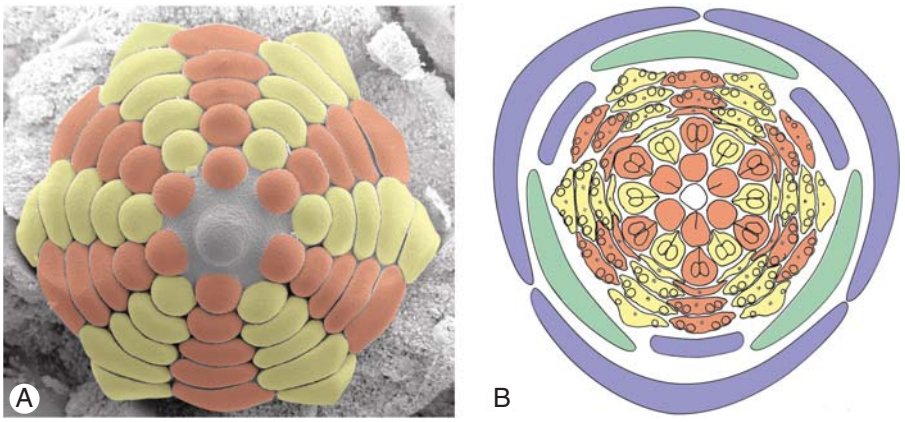

FIG. 3. *Anaxagorea crassipetala*. Floral phyllotaxis. (A) The same flower as in Fig. 1F, with orthostichies in the androecium and gynoecium indicated with colours. (B) Drawing reconstructed of a microtome section of the androecium and gynoecium just before anthesis and tepals added (schematic) to show the organ phyllotaxis of an entire flower. Trimerous whorls (perianth) are coloured blue and green; hexamerous whorls (androecium and gynoecium) are coloured yellow and red.

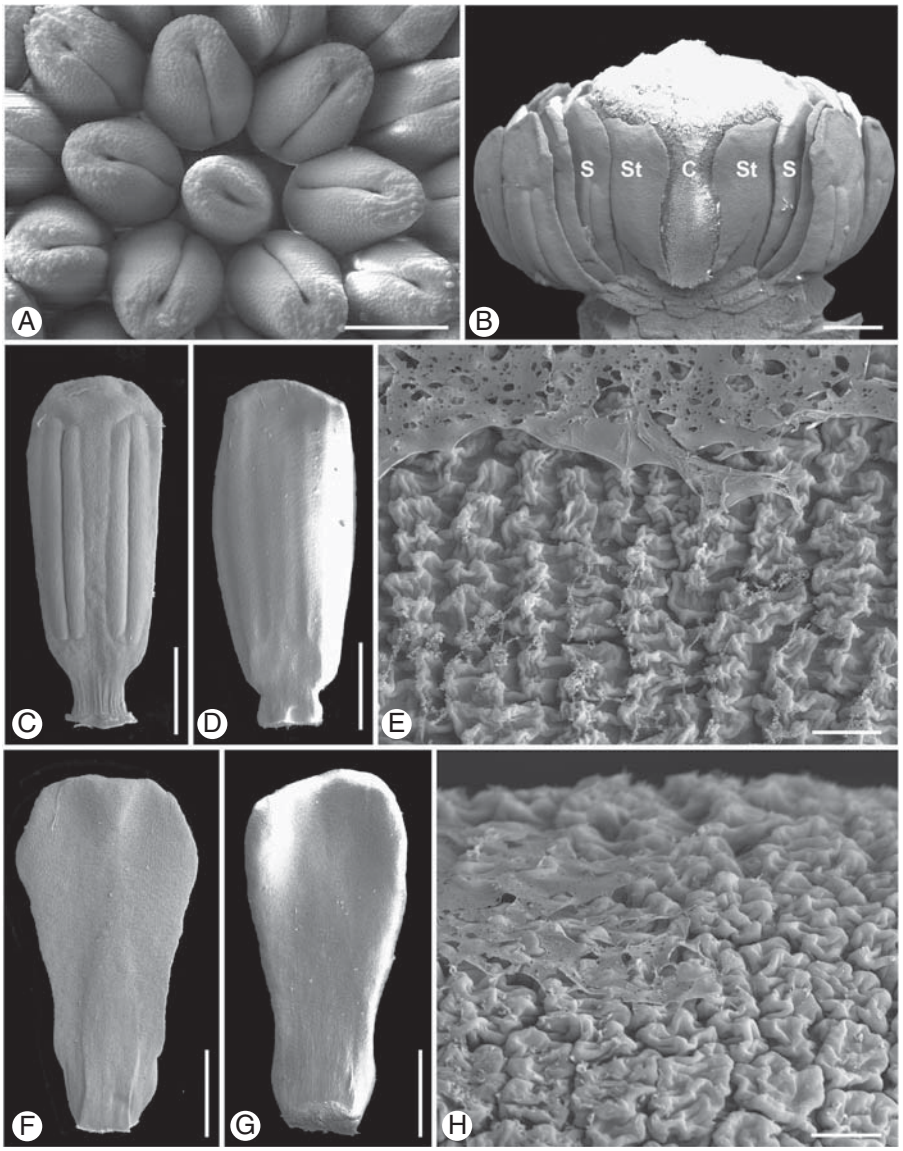

FIG. 4. *Anaxagorea crassipetala*. Scanning electron microscopy micrographs of flowers and floral organs. (A) Centre of the gynoecium of a floral bud. Central carpel surrounded by the six carpels of the third whorl. Funnel-shaped upper part in each carpel beginning to develop. (B) Advanced floral bud from the side, with tepals and part of the stamens/staminodes removed and the stigmatic region appearing white because of charging. (C) Stamen from the dorsal side, with the two elongate thecae and a short filament. (D) Stamen from the ventral side, with pollen sacs of adjacent inner stamen imprinted in the surface. (E) Tip of the stamen with a conspicuously sculpted cuticle, forming narrow protrusions. Secreted material stems from the stigma. (F) Staminode, from the dorsal side. (G) Staminode, from the ventral side. (H) Tip of the staminode with a conspicuously sculpted cuticle, forming broad protrusions. Scale bars: (A) = 100 μm; (B–D, F, G) = 500 μm; (E, H) = 10 μm.

Stamens

The appressed tepal margins create six shallow radial ridges on the floral apex on the orthostichies to which the outermost six stamens belong (Fig. 2C–F). The stamens are initiated centripetally in regular whorls of six (Fig. 2E, F). They are relatively wide from the beginning (Fig. 2E, F). Those of the outermost whorl have a dorsal ridge created by the six gaps where the six tepals of the middle and inner whorl meet (Fig. 2E, F). At anthesis the stamens are flat, 'laminar', pronouncedly extrorse, with a rounded apex and long, parallel thecae (Figs 3B and 4B–D). Each theca opens with two valves. The anther is more than three times as long as the filament (Fig. 4C). Each stamen is served by a single vascular bundle, which branches to both sides above the thecae. As they are contiguous in bud, the stamens within an orthostichy exert some pressure upon each other, and their surface (mainly the adaxial side) has imprints of the relief of the next inner stamens (Fig. 4D). The anthers have short lateral wings in which there is no endothecium. Endothecium is restricted to the pollen sacs, which have a more or less flat surface because of the 'laminar' shape of the stamen. Endothecium cells are larger at the periphery of the theca than close to the stomium and have thin but conspicuous differential thickenings. The septum of each theca is relatively broad

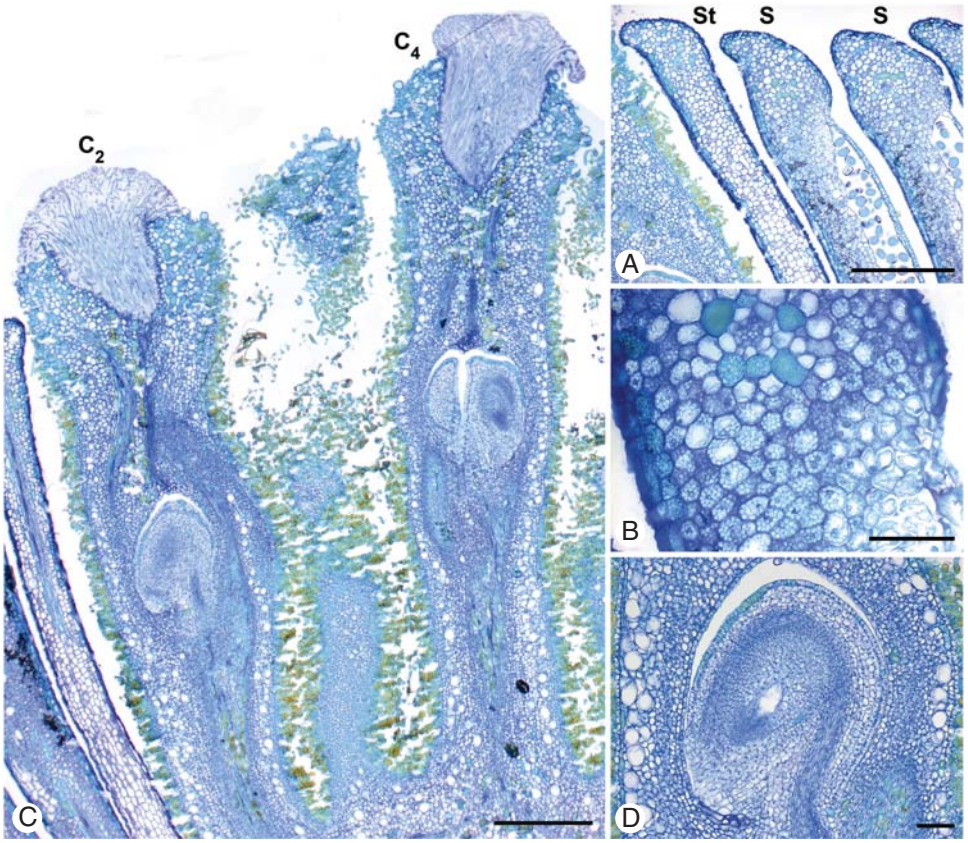

FIG. 5. *Anaxagorea crassipetala*. Longitudinal microtome sections of flowers and floral organs. (A) Tip of two stamens (S) and a staminode (St), showing simple parenchymatic tissue in the staminode and more highly differentiated tissue in stamens. (B) Close-up of the upper region of an anther, showing tissue filled with starch grains. (C) Part of the gynoecium with two hairy carpels, one of the second whorl (C_2) and the central carpel (C_4), showing a funnel-shaped pollen tube transmitting tract in the uppermost area, and narrowing lower down in the style, small ovary, and long stipe. C_2 in approximately median longitudinal section, C_4 in transverse longitudinal section. (D) Ovary with oil cells at the periphery and ovule (approximately median). Scale bars: (A, C) = 500 μm; (B, D) = 100 μm.

(approximately four cell layers). The tissues surrounding the thecae are full of starch. The epidermis and partly the hypodermis and other areas are tanniferous, and there are scattered cells with an oxalate druse and scattered ethereal oil cells (Fig. 5A). The epidermis has a conspicuously sculpted cuticle (Fig. 4E).

Inner staminodes

The six androecial organs of the innermost whorl are sterile and represent inner staminodes. The second innermost whorl is variable, with 0–6 sterile organs (Figs 3B and 4B). The inner staminodes are similar in shape and size to the stamens but they lack thecae (Fig. 4F, G). They are slightly thinner and are histologically less differentiated than the stamens, including the areas outside of the sporangia of the stamens (Figs 3B and 5A). The single vascular bundle does not branch. Compared with the stamens, the staminodes have larger celled parenchyma, especially at the base, and have no starch (Fig. 5A). No secretory tissue is apparent, a histological finding that agrees with the lack of stain retention in fresh flowers. The only part that is slightly more prominent than in the stamens is the somewhat thicker cuticle (appearing black in microtome sections) (Figs 4H and 5A). As in the stamens the epidermis, part of the hypodermis and other areas are tanniferous and have scattered idioblasts with an oxalate druse. Ethereal oil cells appear to be absent.

Gynoecium

Carpel primordia are distinct from stamen primordia by their narrower, more hemispherical shape (Fig. 2F). Each carpel has an unusually long stipe, about as long as the style, which is retained in the unusual explosive fruits (Fig. 5C). The carpels are widest in the upper part, towards the stigma; the ovary is slender (Fig. 6A). The carpels do not have an ascidiate base, but are completely plicate (Fig. 6A, M, N). The ventral slit is even still present for some distance below the ovary locule (Fig. 6M). The carpel in the centre of the gynoecium is also completley plicate. The only difference from the lateral carpels is that its stipe is even longer (Fig. 5C). The uppermost part of the pollen tube transmitting tract is funnel-shaped and consists of long secretory hairs (Figs 5C and 6A–E). These hairs start to develop at a stage shown in Fig. 4A. At anthesis the cell walls of these hairs swell up and produce a gelatinous

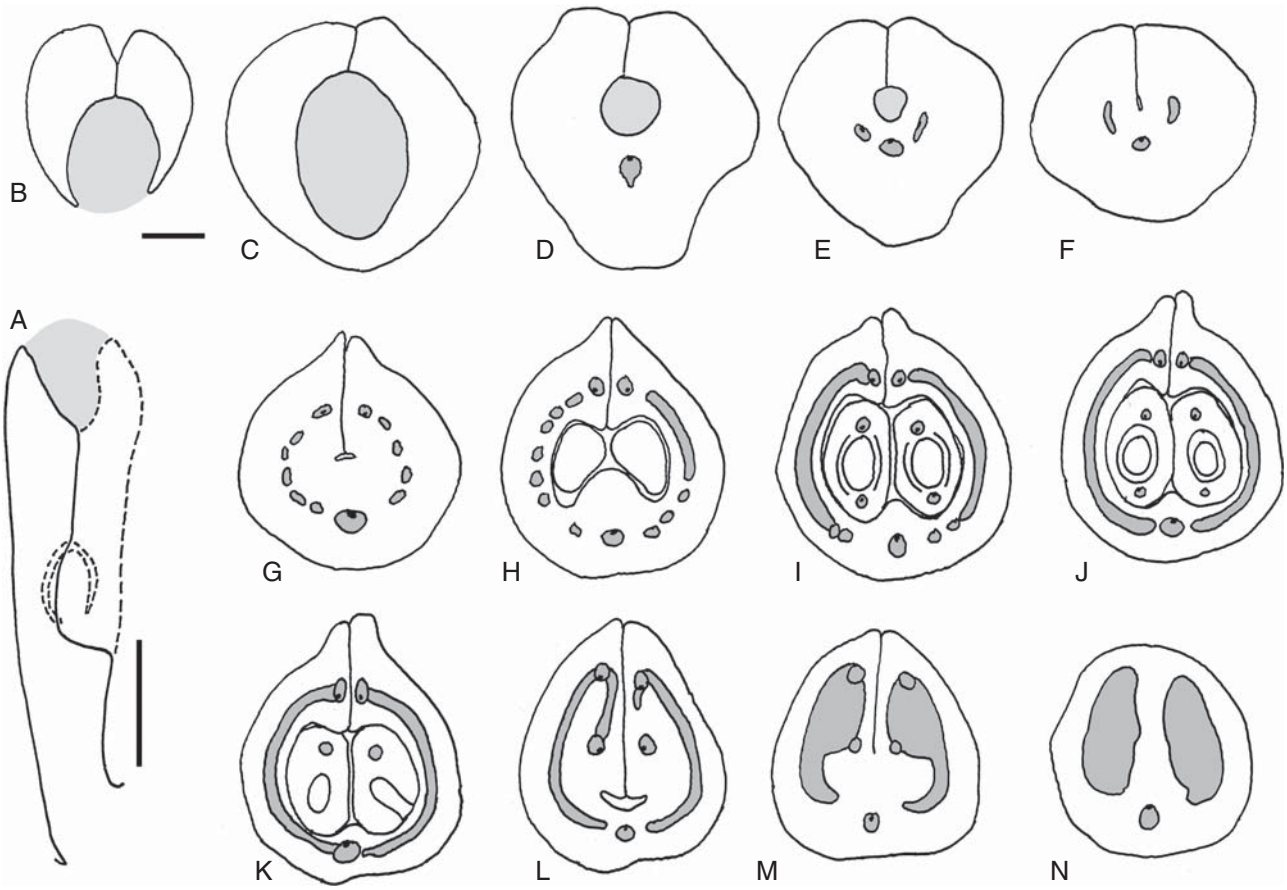

FIG. 6. *Anaxagorea crassipetala*. Drawings of microtome sections of carpels. (A) Schematic median longitudinal section, ventral side at the right. Morphological surface outlined, part in the median plane with a continuous line, part outside of the median plane with a broken line. Funnel-shaped upper part of the pollen tube transmitting tract shaded light grey. (B–N) Transverse section series, from top down, ventral side up. (B) The two lateral tips (ventrally post-genitally united). (C–E) Level of the funnel-shaped pollen tube transmitting tract. (F, G) Lower part of the style with a narrow pollen tube transmitting tract. (H) Upper ovary with the uppermost part of the two ovules. (I) Mid-level of an ovary, perichalazal zone of ovules. (J) Mid-level of an ovary, free zone of integuments. (K) Basal level of an ovary, slightly above the micropyle of the ovules. (L) Basalmost level of an ovary, below the ovule attachment. (M) Below the ovary locule, ventral slit of carpel still present. (N) Level below the ventral slit. Funnel-shaped upper part of the pollen tube transmitting tract shaded light grey. Vasculature outlined and shaded dark grey; distinct vascular bundles within the vascular complex or isolated vascular bundles also outlined; xylem black. Scale bars: (A) = 500 μm; (B–N) = 100 μm.

secretion that protrudes from the apex of the carpels (Figs 1B and 5C). Carpels are covered with clusters of irregularly curved, tanniferous hairs (Fig. 5C). Tanniferous tissue is also associated with the vascular bundles. In the upper part (stigma and upper style) the carpel tissue is large celled, with scattered thick-walled sclereids, and without vascular tissue. Especially in the lower part (lower style, ovary and below), conspicuous oil cells are close to the carpel periphery, most pronouncedly in the hypodermal layer (Fig. 5C). The peripheralmost ones appear to be intrusive.

Each carpel has two lateral ovules with the placentae at the base. The ovules are ascending (Fig. 5D) and the micropyle is directed downwards, towards the placenta and slightly outwards, thus it is slightly syntropous (for this term, see Endress, 2011*a*) (Fig. 6K). The ovules are bitegmic, crassinucellar, anatropous and perichalazal for a short distance (Figs 5D and 6I). Integument thickness is 4–5 cell layers for the outer integument, and three for the inner.

Each carpel has a dorsal vascular bundle and a pair of lateral bundles (Fig. 6E–M). At the level of the ovary, there is, in addition, a continuous band of vascular tissue between the dorsal and lateral bundles, apparently consisting of poorly differentiated (longitudinal) strands (Fig. 6G–L). Below the ovary locule, this band and the lateral bundles form a massive complex of vasculature (Fig. 6M, N). The two ovules are supplied by two additional vascular bundles coming from the massive complex (Fig. 6K–M).

DISCUSSION

Inflorescences and flowers

Flowers in *Anaxagorea* are either single in the axil of foliage leaves (uniflorous inflorescences) or in thyrsoid inflorescences (Fries, 1919, 1940; Scharaschkin and Doyle, 2006). Seemingly uniflorous inflorescences may also be thyrsoid by branching over a longer time span (Scharaschkin and Doyle, 2006). The distinction between the so-called axillary and 'leaf-opposed' patterns within the genus (Fries, 1940; Maas and Westra, 1984) has not yet been worked out sufficiently.

Branching is in median positions, associated with an adaxial prophyll on each branch, as common in many Annonaceae but not in some nested genera (Fries, 1911). This feature also occurs in Eupomatiaceae (Endress, 2003), Degeneriaceae and Himantandraceae, and appears to be a synapomorphy for the clade of these four families (Doyle *et al.*, 2004; Endress and Doyle, 2009) or at least for Eupomatiaceae and Himantandraceae in the topology of Soltis *et al.* (2011). Also ramiflorous or cauliflorous inflorescences as an extreme case of such long-lived inflorescences (cf. Endress, 2010) are common in *Anaxagorea*. Thyrsoid inflorescences and cauliflory are also in accordance with other Annonaceae (Fries, 1949; Weberling and Hoppe, 1996). Likewise, the flowers with relatively bulky floral organs that are tightly contiguous in bud and show conspicuous marks of mutual pressure and superimposed shapes (Endress, 2008) agree with those of the other genera in the family. The extremely fleshy tepals of the second perianth whorl form a resource for non-pollinating florivores (Collier and Armstrong, 2009).

Floral phyllotaxis, organ number and merism

Unlike in other Magnoliales (Magnoliaceae, Himantandraceae, Degeneriaceae, Eupomatiaceae) in which at least in the androecium and gynoecium a spiral phyllotaxis is predominant (Swamy, 1949; Tucker, 1961; Endress, 1977, 1986, 2003; Erbar and Leins, 1982; Zagórska-Marek, 1994; Xu and Rudall, 2006), detailed studies in Annonaceae so far have not shown any instance of spiral floral phyllotaxis. General family descriptions that mention spiral floral phyllotaxis (e.g. Cronquist, 1981; Kessler, 1993; Steinecke, 1993; Takhtajan, 1997) have no factual basis. The case of *Duguetia phaeoclados* with alledged spiral floral phyllotaxis (Maas *et al.*, 2003) has not been documented with a clear analysis. This is also true for *Anaxagorea*, where the indication 'acyclic' (Maas and Westra, 1984) or 'spiral' (Kessler, 1993) is not based on detailed analyses. The Neotropical *A. crassipetala* studied here has regular (complex) whorls. Two additional species cursorily examined from herbarium material in this study also show regular (complex) whorls, one of them A. *luzonensis* from the Old World clade, the other *A. acuminata*, representing another Neotropical sub-clade (Scharaschkin and Doyle, 2006). Myristicaceae are the only other family of Magnoliales with at least partly a non-spiral floral phyllotaxis (even if organs are initiated in a spiral sequence) (Armstrong and Tucker, 1986; Sauquet, 2003). Character optimization in basal angiosperms shows that whorled floral phyllotaxis is an apomorphy for Annonaceae (Endress and Doyle, 2007). The results of the present study fit well with this interpretation.

Despite the apparent lack of spiral patterns, floral phyllotaxis in Annonaceae is quite diverse. A correlation exists between floral organ number and phyllotaxis in the family. The fewer organs there are, the more regularly whorled is the floral phyllotaxis. The more organs there are, the more irregular the phyllotaxis. The minimal (simplest) flowers described in the family have only nine tepals, three stamens and three carpels, such as *Monanthotaxis heterantha* (Baillon, 1868*a*, reported as *Bocagea heterantha*); these organs are in five whorls: three in the perianth, one in the androecium and one in the gynoecium. However, this is somewhat doubtful, as later authors give a minimum of six stamens for the genus *Monanthotaxis* in which this species is now included as *Monanthotaxis heterantha* (Verdcourt, 1971; Johnson and Murray, 1995). The same is also true for the genus *Popowia*, in which this species has been included for some time (Diels, 1925). Thus the question of the minimal stamen number in Annonaceae needs critical re-examination. Species of *Hornschuchia* and *Orophea hexandra* have two stamen whorls (Fries, 1931; Steinecke, 1993; Johnson and Murray, 1995). In other *Orophea* species, flowers have three, six, nine or 12 stamens, and three, six, nine or 12 carpels (Kessler, 1988). However, it is unclear in how many whorls these organs are arranged in flowers with nine or 12 stamens and carpels. Kessler (1988) mentions three stamens and three carpels for *Orophea trigyna* and *O. corymbosa*, but they have in addition three staminodes (apparently outer staminodes as implied by fig. 4a in Steinecke, 1993). In *Miliusa wayanadica* three staminodes are reported to form an outer (?) whorl and three pairs of stamens an inner (?) whorl (Narayanan *et al.*, 2010). In annonaceous flowers with a medium number of stamens, double positions are characteristic (Endress, 1986, 1987; Ronse De Craene and Smets, 1990; Leins and Erbar, 1996; Xu and Ronse De Craene, 2010; for double positions in general, see also Staedler and Endress, 2009). In this pattern, the first stamen whorl has six instead of three stamens, and these alternate pairwise with the preceding innermost tepals. In the following whorls the organs either alternate with the first six stamens or the pattern may be more complicated by triple or multiple positions instead of double positions. Thus the flowers begin development with trimerous whorls and change to hexamerous or even higher-merous whorls in the androecium. The whorls may go back to hexamerous or trimerous (or monomerous) in the gynoecium.

Examples of flowers with relatively few organs and double positions in the first androecial whorl are: *A. crassipetala*: perianth $3 + 3 + 3$; androecium (stamens plus staminodes) $6 + 6 + 6 + 6 + 6 + 6 + 6$; gynoecium, $6 + 6 + 6 + 1$ (this study); and *Monanthotaxis pisocarpa*: perianth $3 + 3 + 3$; androecium $6 + 6 + 6$; gynoecium, $6 + 6$ (P. K.Endress, pers. obs.).

A somewhat more complex pattern is present in *Monanthotaxis whytei*: perianth $3 + 3 + 3$; androecium (stamens plus staminodes), $6 + 9 + 9$; gynoecium, $9 + 9 + 9$ (Ronse Decraene and Smets, 1990). Here two whorls have double positions, with the first androecial whorl resulting in six organs, and the second androecium whorl resulting in nine organs (with double positions only in the radii of the inner perianth whorl) (Ronse Decraene and Smets, 1990).

Documentation of stamen, staminode and carpel numbers for *Anaxagorea* (and other genera of Annonaceae) in the literature is poor, usually just stating 'numerous'. Maas and Westra (1984) at least give ranges of numbers (for 21 of the 26 species treated), but without mentioning most common numbers, and unfortunately rounding the numbers to fives and tens, instead of sixes. Thus, these numbers are not usable for inferences on merism. A single mention of numbers in Fries (1934) is approx. 35 stamens and approx. 25 carpels for *A. pachypetala*. This comes close to the regularly 36 stamens

in *A. crassipetala*, and to 24 carpels, if there were four instead of three carpel whorls. On the other hand, Steinecke (1993, fig. 4b) depicts 53 stamens (including staminodes) (nine whorls?) and 21 carpels for *A. crassipetala* in a schematic figure, and Maas and Westra (1984) give a range of approx. 35–40 stamens, approx. 10–20 staminodes and approx. 10–20 carpels for *A. crassipetala*. Teichert *et al.* (2011) mention 14 ± 2 stamens in the outer whorl, 11 ± 2 staminodes and 12 ± 2 carpels for *A. prionoides*. Globally for the entire genus, Maas and Westra (1984) also provide a range in stamen number (including staminodes) from approx. 10 (*A. brevipedicellata* and *A. floribunda*) to almost 200 (*A. brevipes* and *A. gigantophylla*) and a range in carpel number from five to 45.

The more numerous the stamens (and carpels) become, the smaller are their primordia with respect to the floral apex and therefore they become more prone to positional irregularities. Thus the clear phyllotaxis pattern decays. Such flowers with exceedingly numerous organs (several hundred) and irregular phyllotaxis in the androecium are present in *Monodora* (Leins and Erbar, 1980), and flowers with exceedingly numerous organs and irregular phyllotaxis in both androecium and gynoecium are present in *Annona* (Endress, 2006). Irregular phyllotaxis in polymerous androecia and gynoecia is also found in Magnoliaceae (Tucker, 1961; Zagórska-Marek, 1994; Xu and Rudall, 2006; Zagórska-Marek and Szpak, 2008). Both extremes, genera with only few organs and genera with exceedingly numerous organs, are more or less highly nested in Annonaceae. Thus the basal genus *Anaxagorea*, exemplified here with *A. crassipetala*, is in the middle range, with a medium number of organs and orderly whorls with double positions in the first androecial whorl and subsequent hexamerous whorls, which are continued in the gynoecium.

To summarize, so far not a single case of spiral floral phyllotaxis has been demonstrated in Annonaceae. The flowers are either simple whorled or, most commonly, complex whorled with double positions in the first androecium whorl. In cases with numerous stamens and carpels, the pattern tends to become more complex, with additional double or multiple positions and increased irregularity. Interestingly, it appears that simple whorled floral phyllotaxis in Annonaceae is derived, and the dominant complex whorled pattern with double positions in the outermost androecial whorl and propagation of the resultant hexamerous pattern in the inner whorls, as present in *Anaxagorea*, is primitive in the family.

Perianth and preceding bract

In *Anaxagorea* and in many other Annonaceae the first initiated tepal alternates with the preceding bract (Weisse, 1926). That this bract is sheathing is of interest because a sheathing bract is also present in Eupomatiaceae, the sister of Annonaceae, and in Himantandraceae and Magnoliaceae (Endress, 1977), as well as in Myristicaceae (Armstrong and Tucker, 1986). This widespread presence of sheathing bracts in Magnoliales may be a pre-condition for the evolutionary loss of the perianth in Eupomatiaceae and Himantandraceae (Endress, 1977, 2003; Doyle and Endress, 2000; Kim *et al.*, 2005) and concomitant with a further elaboration of the sheathing bract. Whether the sheathing bract in *Anaxagorea* is a prophyll or an additional bract between the prophyll and the first tepal needs to be studied.

Stamens

The flat, 'laminar', pronouncedly extrorse stamens of *A. crassipetala* are reminiscent of those of *Degeneria* in their proportions (Bailey and Smith, 1942; Endress and Hufford, 1989). In other *Anaxagorea* species stamen shape is more different (Scharaschkin and Doyle, 2006). As in other Annonaceae (Endress, 2008), in *Anaxagorea* the stamens are contiguous in floral bud, and their ventral surface has imprints of the relief of the thecae of the next inner stamens. However, stamen shape is not hexagonal as in more derived clades of Annonaceae. The dehiscence line of each theca is H-shaped, resulting in two opening valves as in other Annonaceae, as well as in Eupomatiaceae, Himantandraceae, Degeneriaceae and Magnoliaceae (Endress and Hufford, 1989; Endress, 2011*b*).

Inner staminodes

Inner staminodes are mostly secretory where they occur in Magnoliales, such as in Eupomatiaceae, Himantandraceae, Degeneriaceae (Endress, 1984*b*) and some species of *Anaxagorea* (Scharaschkin and Doyle, 2005, 2006). However, the staminodes of *A. crassipetala* are not secretory (this study; Scharaschkin and Doyle, 2006) and have a simple histology. In *A. crassipetala* the staminodes have the same length as the stamens and do not appear to have an obvious function (J.E. Armstrong, pers. obs.). However, in a few other species of *Anaxagorea* the staminodes overtop the stamens and carpels, at least by the end of the female phase, and so form a physical barrier between androecium and gynoecium and potentially function in herkogamy (*A. javanica*, Corner, 1940; Maas and Westra, 1984; *A. dolichocarpa*; Maas-van de Kamer, 1993; and *A. brevipes*; Webber, 2002), as is also the case in those of Eupomatiaceae, Himantandraceae and Degeneriaceae (Endress, 1984*b*). The presence of inner staminodes may be a synapomorphy of these four families within Magnoliales or a synapomorphy of Laurales and Magnoliales, with a loss in Myristicaceae and Magnoliaceae (Doyle and Endress, 2010, 2011).

Gynoecium

In Annonaceae commonly the carpels are completely plicate, and the ventral slit may continue for some distance along the stipe below the locule (Deroin, 1988; Briechle-Mäck, 1994; Igersheim and Endress, 1997). However, a short ascidiate zone was found in species of a few genera by Deroin (1988), such as *Anaxagorea* (*A. luzonensis*, table XXX, fig. 5), *Cananga* (*C. odorata*, plate XXXIV, fig. 2), *Uvaria* (*U. scabrida*, plate XXXI, fig. 11) and *Xylopia* (*X. aethiopica*, plate XXX, fig. 14). This distribution of peltate carpels (i.e. carpels with an ascidiate base) among the basal genus *Anaxagorea* and three other genera, one of which, *Cananga* (ambavioid clade), is also relatively basal (Surweswaran *et al.*, 2010; Couvreur *et al.*, 2011), may suggest peltate carpels to be plesiomorphic in Annonaceae.

However, the present finding that in *A. crassipetala* the carpels are completely plicate, as in the majority of Annonaceae, does not further support this view. It would be interesting to know whether this is an important difference between the Old World and New World clade of *Anaxagorea*.

In *Anaxagorea* the carpels have three distinct longitudinal vascular bundles, a dorsal bundle and two ventral ones, and there are horizontal connections between them, as described for other Annonaceae (e.g. *Cananga*; Periasamy and Swamy, 1956). In *Anaxagorea* these connections form a dense band of vasculature, still immature at anthesis. The potential role of this band in the dehiscence of the explosive fruits is unknown. The ovules are served by the lateral bundle complex from the base of the carpel, as also shown for *A. luzonensis* (Deroin, 1997). This differs from other genera, in which the ovules have been described to be served from separate vascular bundles departing directly from the dorsal bundles (such as *Cananga*, Periasamy and Swamy, 1956; *Saccopetalum*, Sastri, 1957; and *Piptostigma*, Deroin, 1997), or from relatively dorsally positioned bundles of the lateral network of bundles (such as *Meiocarpidium*, Deroin, 1987; and *Ambavia*, Deroin and Le Thomas, 1989). Whether these descriptions of direct dorsal connections are correct may only be decided by more detailed developmental studies. Tanniferous tissue at the periphery is a common feature in angiosperms. Intrusive ethereal oil cells are common in a number of basal angiosperms (e.g. Endress and Igersheim 2000).

Conclusions

The study of floral phyllotaxis in *Anaxagorea* shows that there is no signature of basal spiral floral phyllotaxis in Annonaceae. Similarly, the carpels of *A. crassipetala* do not have an ascidiate base, in contrast to those of *A. luzonensis* studied by Deroin (1988). Thus the family appears uniform in its whorled (to irregular) floral phyllotaxis, with double positions in the first stamen whorl and almost uniform in its completely plicate carpels. These features may be apomorphies for Annonaceae, as they are not present in Eupomatiaceae, Degeneriaceae and Himantandraceae. The only floral features studied that may be plesiomorphic in *Anaxagorea* and no longer present in most Annonaceae are the flat stamens, and perhaps the presence of inner staminodes. Thus the floral structure of Annonaceae is macrosystematically quite homogeneous, and the diversity results from apomorphies within the family.

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